ZOOLOGICAL SCIENCE 8: 983–989 (1991)

Thermoregulation and Habitat Preference in Two Wing Color Forms of *Mnais* Damselflies (Odonata: Calopterygidae)

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ABSTRACT—Thoracic temperatures of *Mnais* damselflies with wing color dimorphism (pale orange vs hyaline) were compared with ambient and radiation temperatures. All sexually immature adults remained on perches in sunflecks in deciduous forests. They controlled their thoracic temperature against radiant heat load in similar manner. After maturation, territorial males, with orange wings, were seen to spend much time perching in open streams, increasing the degree of thermoregulation. They changed some physiological properties, probably due to the quantity of haemolymph because of decline in water content of the thorax. Although there was a similar decline in water content of mature females, with orange wings, change in the body temperature did not show higher degree of thermoregulation because of their perching behavior for mating in open streams. Both sexes of mature insects with hyaline wings were restricted to deciduous forests. Their water content ratio did not vary with ageing. The response of controlling thoracic temperature to ambient and radiation temperature was similar to that in immature adults. The high degree of thermoregulation clearly allowed mature insects with orange wings to be active under direct sunlight.

INTRODUCTION

Thermoregulation is an important behavioral activity in adult Odonata. Since they spend much time in sunlight, in either open or closed habitats [1–2], any behavior that regulates body temperature would be advantageous. Some peculiar postures such as an "obelisk" are those used for regulation of thoracic temperature against solar radiation [3]. In low temperatures they shiver or whir their wings for basking [4].

Based on the means of thermoregulation, "fliers" and "perchers" were recognized in Odonata considering their active period on the wing [5]. Soaring or gliding in high temperatures is commonly seen in the former type of species. Their heat transfer between abdomen and thorax by haemolymph was clarified [4]. The energy metabolism for soaring flight was similar to the resting metabolism because wings are essentially immobile [6]. On the other hand, in the latter type of species perched under direct sunlight. However, there was no evidence of heat transfer in the body [7].

The Japanese *Mnais*-species is regarded as a percher. It shows a remarkable polymorphism including wing polychromatism in both sexes and a complicated geographical variation in Japan. Wing dimorphism and differences in habitat preference have been considered to be an adaptation for thermoregulation in *Colias* butterflies [8]. In the present study, I compared wing polymorphism for the thermoregulation againt solar radiation and ambient temperature in relation to ageing, and discussed their habitat preference. The water content in their thorax is also measured as an indicator of the quantity of haemolymph.

MATERIALS AND METHODS

Two distinct forms with pale orange and hyaline wings in *Mnais*-species have been recognized for both sexes in Tsu, Mie Prefecture, central Honshu, Japan [9]. The orange-winged damselflies mainly inhabit open fields where some males hold territories. They belong to *M. pruinosa nawai* Yamamoto, according to Asahina [10]. On the contrary,

Accepted April 25, 1991
Received January 14, 1991

hyaline-winged damselflies always stay in closed habitats such as sunflecks on forest floors. They still have no scientific name (*Mnais* sp.) but have a Japanese name, Hiura-kawa-tombo [11]. They do not show clear territorialism. Since it has been included in some different classificatory systems by certain taxonomists [10, 12], in this paper, I have adopted the wing color division for referring to each group of *Mnais*-damselflies.

The survey area was located in Tsu, Mie Prefecture. It includes paddy fields and a deciduous forest with various sizes of sunflecks. Study plots were prepared along a stream in the paddy fields (300 m long) and in the forest (400 m long). The former is an open habitat, where the stream is 1 m wide. Study plots with a 5 m width were set up on either side of the stream. The latter is a shaded habitat, where the study plots were set up 50 m on either side of a stream less than 1 m in width.

The field survey was made on 20 windless and sunny days between 28th April and 1st July, 1988. On each sampling day, I surveyed along the stream and on the paths of the neighboring forest floor.

The thoracic temperature of the damselflies was measured chiefly during the period between 08:00 and 17:00, because mature males arrived in the stream or sunflecks from roosting sites after 08:00 and left at around 16:00 [13]. All the damselflies found were captured by a net after recording their perching postures. The thoracic temperature was measured within 10 sec from the time of capture. If the time from capturing to measuring exceeded 10 sec, or if I touched their thorax or abdomen, the damselfly was marked and released without measuring. A pocketable digital thermometer (accuracy 0.1°C) with a thermocouple probe of 0.5 mm in diameter was used for measuring the thoracic temperature. Damselflies in the state of feeding, flying, ovipositing or copulating were not recorded.

Immediately after measuring the thoracic temperature (about 1 min), ambient and radiation temperatures were measured at the same perching point. An Assmann's aspiration psychrometer was used for measuring the former. A digital thermometer with a sensor covered with black tape was used for measuring the latter.

The degree of wing wear and the color of the abdomen were recorded in order to obtain information on ageing. In the present study, the damselflies were divided into two age classes: sexually immature and sexually mature.

All the damselflies whose thoracic temperature was measured were brought to the laboratory and their abdomen and hind wing lengths were recorded. Then, the thorax of each individual was removed and weighed (accuracy 0.1 mg) to assess the water content of the body. The samples were then dried in a homoiothermal chamber under 80°C for 8 hr and re-weighed.

RESULTS

Size and water content of the damselflies

Either body size or quantity of haemolymph may affect thermoregulation. Table 1 shows that orange-winged damselflies were larger than hyaline-winged ones in both sexes. The abdomen length of mature orange-winged males was significantly larger than that of immature one, whereas their hind wing length was not significatly different in either stage.

An orange-winged damselfly was heavier than a hyaline-winged one. Mature orange-winged males were the heaviest. With ageing, the dry weight of the thorax increased, and the water content ratio of the thorax decreased, particularly in the orange-winged form. In hyaline-winged damselflies, the water content ratios were similar in the two age classes.

Thermal environment of perching sites

During the survey period, the ambient temperature in the open stream varied from 15.1°C to 29.2°C, and that of the radiation temperature from 23.5°C to 42.7°C. The regression coefficient between the radiation and the ambient temperature was 1.40 ($r^2=0.98$, $n=112$), which is significantly different from unity ($P<0.001$). This shows that the rate of increase of the radiation temperature was higher than that of the ambient temperature.

On the other hand, the ambient temperature at the sunflecks in the deciduous forest was relatively low, ranging from 11.7°C to 28.7°C, and that of the radiation was from 14.4°C to 40.6°C. The radia-

TABLE 1. Size, dry weight, and water content of the thorax in different wing forms of the *Mnais*-damselflies on aging. Each mean was assesed by ANOVA between the ages

Wing-form	Sex			Immature stage	Mature stage	
Orange	♂	abdomen length	(mm)	45.3±1.0 (40)	47.7±0.2 (54)	P<0.01
		hind wing length	(mm)	38.7±0.3 (39)	39.4±0.2 (54)	n.s.
		dry weight	(mg)	66.9±4.4 (27)	108.8±2.1 (50)	P<0.01
		water content	(%)	78.0±0.8 (27)	71.8±0.6 (50)	P<0.01
	♀	abdomen length	(mm)	41.3±0.2 (93)	41.9±0.4 (20)	n.s.
		hind wing length	(mm)	38.7±0.2 (94)	38.8±0.5 (20)	n.s.
		dry weight	(mg)	61.3±2.3 (82)	73.7±3.4 (19)	0.05>P>0.01
		water content	(%)	78.7±0.5 (82)	73.8±1.4 (19)	P<0.01
Hyaline	♂	abdomen length	(mm)	42.6±0.4 (41)	43.2±0.3 (37)	n.s.
		hind wing length	(mm)	34.1±1.8 (41)	34.7±0.2 (36)	n.s.
		dry weight	(mg)	42.0±2.1 (35)	64.0±2.2 (37)	P<0.01
		water content	(%)	78.3±0.8 (35)	77.1±0.6 (37)	n.s.
	♀	abdomen length	(mm)	38.9±0.3 (46)	39.2±0.4 (17)	n.s.
		hind wing length	(mm)	35.9±0.3 (46)	35.5±0.6 (17)	n.s.
		dry weight	(mg)	45.4±0.2 (37)	61.3±3.7 (16)	P<0.01
		water content	(%)	78.0±0.6 (37)	75.5±1.8 (16)	n.s.

( ): Number of damselflies sampled.

TABLE 2. Regression coefficient (b) and determination coefficient (r^2) of the thoracic on the ambient temperature of different wing forms of the *Mnais*-damselflies on ageing. Each regression coefficient was assessed by a t-test with b=1

Wing-form	Sex	Perching site	Immature stage				Mature stage			
			b	r^2	n		b	r^2	n	
Orange	♂	sunfleck	0.98	0.93	10	n.s.	—	—	0	
		open	0.95	0.82	22	n.s.	0.66	0.31	21	n.s.
	♀	sunfleck	0.75	0.78	50	P<0.01	—	—	0	
		open	—	—	0		0.66	0.58	8	n.s.
Hyaline	♂	sunfleck	0.67	0.73	20	P<0.01	0.82	0.60	7	n.s.
	♀	sunfleck	0.73	0.74	24	P<0.01	0.80	0.45	6	n.s.

n: Number of damselflies sampled.

tion temperature fluctuated more widely than that of the open stream, according to the differences in the size of sunflecks and its surrounding vegetation. The regression coefficient between the radiation and ambient temperature was 0.98 (r^2=0.32, n=120), which is near unity.

Thoracic temperature against ambient and radiation temperature

Most damselflies with orange or hyaline wings began to emerge in late April in the open stream in the study area. They stayed only one day there before moving to deciduous forests near the stream. Their sexually immature stage was 1 to 2

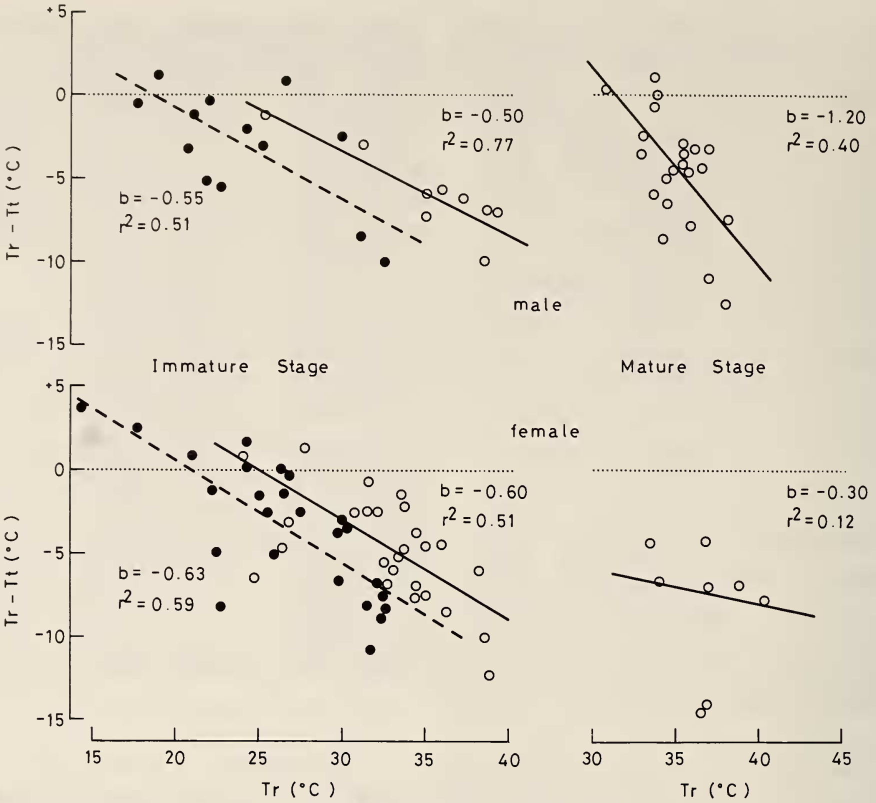

Fig. 1. The relationship between the radiation temperature (Tr) and the odds with the thoracic temperature (Tr-Tt) in the damselflies of orange-winged forms. An open circle represents a damselfly perching in open sites; a solid circle represents a damselfly perching in sunflecks.

weeks. After maturation, the orange-winged males held territories in the open stream. Mature males of the hyaline-winged form flew around the deciduous forest floor and over the shaded stream. Therefore, no encounter between the orange- and hyaline-winged forms was observed in the study area.

The thoracic temperature was always higher than the ambient temperature (max. ca. 10°C) irrespective of perching postures. The relation between thoracic and ambient temperatures was almost linear (Table 2). However, all the regression coefficients were below unity, though two thirds of the coefficients were not significantly different from unity.

Radiant heat load might effectively contribute to increasing the body temperature of damselflies perching under direct sunlight. If there is a certain mechanism for thermoregulation against radiant energy, the rate of increase of thoracic temperature may be expected to be lower than that for the radiation temperature. If so, the regression coefficient of the odds on the radiation temperature must be negative. Further, the regression coefficient itself may be used as an index of thermoregulation ability of damselflies.

In the immature damselflies of the orange-winged form, the regression coefficient was almost -0.5 or -0.6, irrespective of the differences in the condition of perching point, either in sunflecks or at the open stream (Fig. 1). On the contrary, there is a salient sexual difference in mature individuals. The regression coefficient in mature males was -1.20 ($r^2=0.40$): the rate of increase of the thoracic temperature with the radiation temperature was the lowest. This means that the body temperature is kept relatively low under high ambient temperatures. However, such a relation

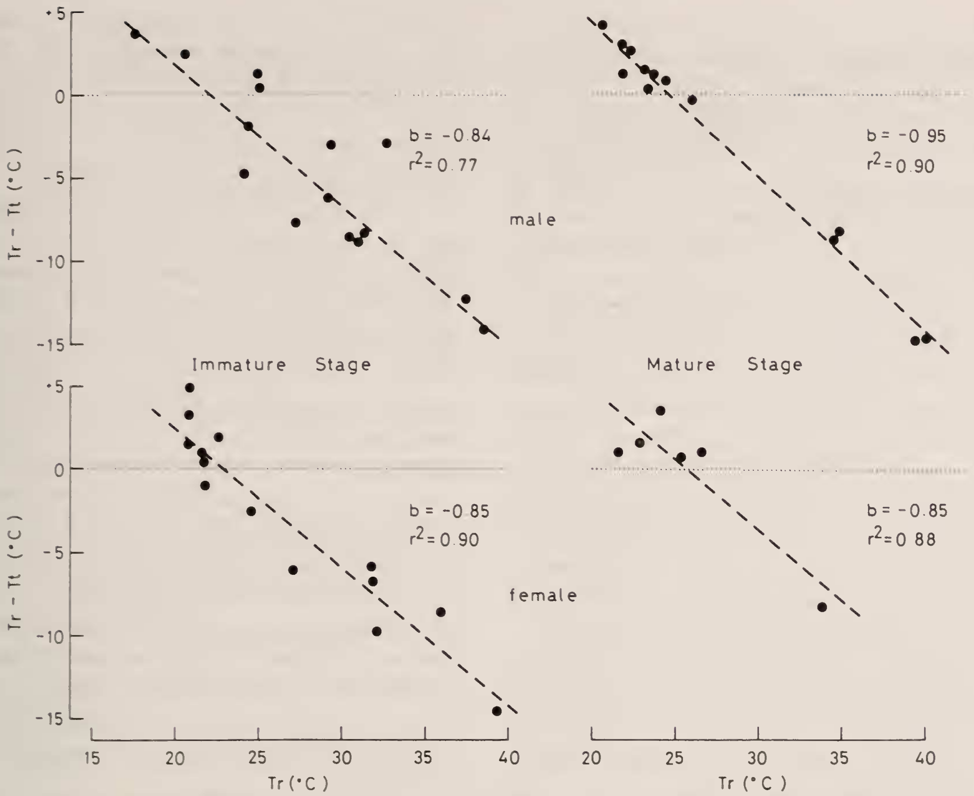

FIG. 2. The relationship between the radiation temperature (Tr) and the odds with the thoracic temperature (Tr-Tt) in the damselflies of hyaline-winged forms perching in sunflecks.

was obscure in females.

The regression coefficients in the damselflies of both sexes of the hyaline-winged form were smaller than those in the orange-winged one during the immature stage of both sexes (Fig. 2).

DISCUSSION

After emergence, damselflies take several days to mature [14]. Although the preferable habitats of orange- and hyaline-winged damselflies differ in their mature stage [11, 15], they were both restricted to deciduous forests during their immature stage. Most immatures perched in sunflecks. The size of sunfleck and its surrounding vegetation varied as noted above [2]. The thermal environment of the sunflecks, particularly radiation temperature, varied according to different sunflecks. The change of radiation temperature can, however, be roughly explained by the ambient temperature. Therefore, the change in the ambient temperature might affect the body temperature of damselflies inhabiting the forest as well as radiation. However, radiation temperature seemed to be more important for the damselfly perching in the open stream than the ambient temperature.

Although damselflies are poikilotherms, their body temperature is probably regulated against both ambient and radiation temperatures. Several works on thermoregulation have so far focused on the radiant heat load obtained from a thermister with a probe painted black [4, 16–18]. The behavioral posture for thermoregulation against radiation was analyzed in many butterfly species [18–19]. However, the perching posture of the damselfly species, excepting the "obelisk", has not so far been studied from the aspect of thermoregulation [3]. In general, conductive heat transfer between the wing base and the thorax is negligible

[20].

Other elaborate physiological adaptations, as well as perching behavior, also help odanate species to regulate body temperature [21–22]. Control of haemolymph in thermoregulation may be important in damselflies as in some butterfly species [19]. The "fliers" appeared to thermoregulate exclusively through controlling blood circulation [7]. In general, most flying insects have higher rates of metabolism, and hence heat production, than other animals [23]. Rapid rates of cooling, due to their small size, may preclude appreciable endothermy. Since the *Mnais* damselfly is a percher that stays under direct sunlight all day long, controlling the radiant heat load may be a more important factor for body temperature than that in the fliers. They receive solar input onto the body without heat loss due to wind. Furthermore, I observed no endothermic behavior, probably as no cool days occurred during the survey period.

Teneral damselflies thermoregulate poorly due to their cuticle being incompletely hardened [4]. This suggests that both orange and hyaline wing forms might have the same thermoregulatory mechanism during their immature stages. This is subject to excessive water loss. The water content ratio of the thorax in immature damselflies was similar irrespective of the difference of wing form, though body size was significantly different.

It is reasonable to find that the relationship between thoracic temperature and radiation or ambient temperature was similar in both wing forms, if the water content simply reflects the haemolymph content. However, the water content: thorax weight ratio decreased in mature orange-winged males. Therefore, the growth rate of inner parts of the thorax, mainly the muscles for flight, was high. This may be advantageous to the males because they must stay in open sites to maintain their territories. This might be lower the heat exchange rate from the abdomen to the thorax, though male postural adjustments for avoiding overheating might also be effective. They might then change their body physiology in order to stay in open fields. However, mature females showed a little change in their body physiology, probably due to their behavior. Mature females perching under direct sunlight were sampled irrespective of their previous behavior: some of them had just finished oviposition (the thoracic temperature of the females might be relatively low because they were sometimes sprayed by the stream during oviposition) and others were oriented towards the territory to mate.

On the other hand, hyaline-winged damselflies did not change their water content ratio. The regression coefficients suggest that hyaline-winged damselflies have a relatively steady thermoregulation mechanism against high radiant heat load. Such a mechanism seemed to be unrelated to age because the regression coefficients at both stages were not markedly different in either sex. In Kyushu, however, male f. *strigata* with hyaline wings of *M. p. pruinosa* settled around the territories of f. *esakii* with orange wings of *M. p. pruinosa* in open streams [24–25]. Such males with hyaline wing must perch under direct sunlight. It is said that a certain change in the body physiology of f. *strigata* in respect to thermoregulation between immature and mature stages seemed to occur. Thus, thermoregulation may be influenceed by the thermal environment of the mating sites of the damselflies.

ACKNOWLEDGMENTS

This study was supported primarily by grants from Nissan Science Foundation. I am especially indebted to Mr. Ko'ichi Tanabe for his continued assistance in the field. Drs. Kazunori Higashi, Kunio Suzuki and Keisuke Ueda read earlier drafts of the paper and offered helpful comments. Mr. Naoyuki Ohsawa identified the damselflies. I also thank Mr. Masao Taguchi for useful discussions.

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